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Realizing the potential of trait-based approaches to advance fisheries science

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Abstract

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30 Analyzing how fish populations and their ecological communities respond to perturbations such
31 as fishing and environmental variation is crucial to fisheries science. Researchers often predict
32 fish population dynamics using species-level life-history parameters that are treated as fixed over
33 time, while ignoring the impact of intraspecific variation on ecosystem dynamics. However,
34 there is increasing recognition of the need to include processes operating at ecosystem levels
35 (changes in drivers of productivity) while also accounting for variation over space, time, and
36 among individuals. To address similar challenges, community ecologists studying plants, insects,
37 and other taxa increasingly measure phenotypic characteristics of individual animals that affect
38 fitness or ecological function (termed “functional traits”). Here, we review the history of trait-
39 based methods in fish and other taxa, and argue that fisheries science could see benefits by
40 integrating trait-based approaches within existing fisheries analyses. We argue that measuring
41 and modeling functional traits can improve estimates of population and community dynamics,
42 and rapidly detect responses to fishing and environmental drivers. We support this claim using
43 three concrete examples: how trait-based approaches could account for time-varying parameters
44 in population models; improve fisheries management and harvest control rules; and inform size-
45 based models of marine communities. We then present a step-by-step primer for how trait-based
46 methods could be adapted to complement existing models and analyses in fisheries science.
47 Finally, we call for the creation and expansion of publicly available trait databases to facilitate
48 adapting trait-based methods in fisheries science, to complement existing public databases of
49 life-history parameters for marine organisms.

50 *Keywords:* community ecology, ecosystem-based fishery management, functional trait,
51 population dynamics, size-spectrum, stock assessment

52 **1. What is trait-based ecology and why might it be useful in fisheries?**

53 Trait-based analysis involves analyzing ecological dynamics using measurable characteristics of
54 individuals instead of average demographic rates estimated for the population to quantify
55 changes in status of ecological communities. Here, we briefly review advances in trait-based
56 ecology and explain how these novel insights and methods could improve fisheries management.
57 We argue that trait-based approaches offer solutions to three major challenges in modern aquatic
58 conservation and fisheries science, particularly those related to implementing ecosystem-based
59 management:

60 1. accounting for time-varying processes in resource assessments (section 2.1);

- 61 2. assessing the status and dynamics of communities (sections 2.2, 3.3); and
62 3. determining harvesting strategy at the community scale (sections 1, 2.2, 3.3).

63 We describe a framework to address these challenges with trait-based approaches (section 3) and
64 propose specific actions to execute the framework (section 4). Rather than a complete synthesis,
65 we focus on a set of examples where trait-based approaches could be applied to management
66 most seamlessly or with greatest benefit.

67 To distinguish trait-based approaches from the population-based methods typically
68 employed in fisheries science, we define a trait as any characteristic of the phenotype that could
69 affect ecological function or performance and can be measured on an individual sampled at a
70 single moment in time. Common examples of traits are measures of morphology, physiology,
71 and phenology. Confusion about the specific definition of a trait persists in the primary literature,
72 where some include population-level quantities such as the finite rate of population increase
73 (Violle et al., 2007), or life-history characteristics that are asymptotic expectations of some
74 individual trait. Our trait definition follows the stricter, though commonly applied ecological
75 definition of something individually measurable and functional, i.e., traits that influence fitness
76 through their relationship with growth, reproduction and survival (McGill, Enquist, Weiher, &
77 Westoby, 2006). This is different than quantities like maximum body length, which is a
78 population-level parameter (see Table 1 for examples of traits and parameters).

79 Trait-based methods are deepening the understanding of community ecology beyond that
80 established by more traditional, population- or species-based approaches (McGill et al., 2006;
81 Violle et al., 2007). This is particularly true with respect to understanding the influence of biotic
82 and abiotic factors on processes regulating community structure and how this affects predicted
83 responses of ecosystem functions and services to environmental change (Kjørboe, Visser, &
84 Andersen, 2018; Lavorel & Garnier, 2002; Litchman, Pinto, Klausmeier, Thomas, & Yoshiyama,
85 2010; McGill et al., 2006; Mouillot, Graham, Villéger, Mason, & Bellwood, 2013). Traditional
86 approaches that focus on comparing point-values of species parameters will likely underestimate
87 the effect of species on one another due to niche overlap (by not properly accounting for niche
88 breadth), and thus are poor predictors of how communities will respond to change (Violle et al.,
89 2012). Trait-based methods provide a way to quantify population and community structure by
90 accounting for variability among individuals in a common currency across levels of ecological
91 organization (i.e., trait variation or diversity). Predicting how fitness changes with environmental

92 variation is a common goal across many fields of ecology, including fisheries, where researchers
93 attempt to translate the effect of environmental fluctuations on individual organisms across the
94 food web to changes in vital rates and stock productivity. Fitness-environment relationships are
95 typically estimated from observed correlations and are unlikely to remain consistent over space
96 and time (Deyle et al., 2013; Holt & Gaines, 1992). Traits provide a mechanistic basis for
97 developing fitness-environment relationships, and therefore show promise for predicting
98 population and community responses to environmental change (Laughlin & Messier, 2015).

99 Fisheries science faces similar challenges to community ecology given increasing calls to
100 incorporate assessments of ecosystem status and dynamics into policy through ecosystem-based
101 fishery management (EBFM). As EBFM has created a desire to incorporate species interactions
102 into management decisions, the natural first step is to quantify pairwise trophic interactions
103 grouped by taxonomy and ignore within-group variation as in classical community ecology
104 theory (Bolnick et al., 2011). However, we know that trait variation within species is often broad
105 and similar to that among species (Kattge et al., 2011; Messier, McGill, & Lechowicz, 2010).
106 Further, intraspecific trait change has a comparable effect to interspecific change in terms of
107 influence on community biomass, structure, and function (Des Roches et al., 2018). For example,
108 trophic level of North Sea fishes is well explained by individual body size when summarized at
109 the community scale, but not when size is summarized by species (Jennings, Pinnegar, Polunin,
110 & Boon, 2001). Despite the clear ecological significance of intraspecific variation, it is not often
111 monitored (Mimura et al., 2017). When individual traits are measured, the intraspecific variation
112 is often lost in the analysis stage. Inference can change greatly depending on whether
113 intraspecific variation is available to provide context (Bolnick et al., 2011; Des Roches et al.,
114 2018), for example, when attempting to discriminate species based on general phenotypic
115 characteristics (Fig. 1). Trait-based approaches incorporate intraspecific variation, an important
116 consideration given the magnitude and role of such variation in population and community
117 stability (Mimura et al., 2017), for example, through effects on the diversity of responses to
118 environmental variation (Barnett, Baskett, & Botsford, 2015; Bolnick et al., 2011; Elmqvist et
119 al., 2003; Schindler et al., 2010). Although increasing population and community stability is not
120 often an explicit goal of traditional single-species fishery management, it is an objective of
121 EBFM, and reducing variability in productivity and exploitable biomass can provide large
122 socioeconomic benefits to fishing communities (Badjeck, Allison, Halls, & Dulvy, 2010;

123 Sanchirico, Smith, & Lipton, 2008; Sethi, 2010). Trait-based approaches will likely improve
124 assessment of the structure and dynamics of ecosystems and interpretation of the effect on
125 services (i.e., sustainable fisheries).

126 One critical challenge for the theory underlying EBFM is predicting which harvest
127 policies are most efficient at the ecosystem level, i.e., those that best satisfy a trade-off between
128 maximizing fishery yield or profit and producing a desired community state (e.g., a sustainable
129 biomass level) (Andersen, Brander, & Ravn-Jensen, 2015; Jacobsen, Burgess, & Andersen,
130 2017). For example, traditional population-based perspectives on optimal multispecies fishery
131 management typically suggested that the pathway to efficiency was selective targeting of only
132 the most productive and marketable species at mature sizes; however, contradictory results from
133 modern ecosystem models have led some researchers to the conclusion that unselective fishing,
134 or harvesting all species and sizes in proportion to their productivity would produce better
135 outcomes (Garcia et al., 2012). This question of whether and how to selectively fish is best
136 addressed with trait-based ecosystem models of individual size. Fish vital rates are most affected
137 by size, and body size also determines the distribution of abundance among marine species
138 (Sheldon and Parsons 1967, Sheldon et al., 1970) through basic physiological constraints of
139 predator-prey interactions (Andersen & Beyer, 2006). Recently-developed community models
140 using individual size as a functional trait are providing general insights for multispecies harvest
141 strategies (Andersen, Brander, et al., 2015; Jacobsen et al., 2017; Jacobsen, Gislason, &
142 Andersen, 2014), and we expect that development and use of similar trait-based models will be
143 critical for designing specific policy actions and evaluating their performance toward the
144 implementation of EBFM.

145 We assert that adopting trait-based approaches would generate rapid advances in fisheries
146 science, improving our estimation and understanding of fish population and ecosystem
147 dynamics, and influence fisheries management decisions. From an extreme perspective, this
148 could mean using functional classifications arising from similarities in phenotypic characteristics
149 at the individual scale rather than population or taxonomic (e.g., species) levels. More
150 realistically, given the structure of established fishery management regimes and the
151 corresponding organismal scale of questions in this field, trait-based approaches will likely
152 supplement—not usurp—the traditional population-based approach. We propose integrating
153 trait-based perspectives into existing management frameworks to reveal how trait distributions

154 are likely to bias population-level measures of productivity and modify optimal harvesting
155 strategies. In addition, trait-based approaches could help by creating novel methods to address
156 major challenges for EBFM. Trait-based approaches are especially suited for addressing these
157 challenges, enabling incorporation of temporal variation in growth, reproduction and survival
158 into assessments of resource productivity and status via rapid, spatially-explicit, direct
159 measurements at the individual level where interactions and their consequences are realized. As
160 the scope of fisheries science expands from populations to ecosystems, we must learn from
161 community ecology. To this end, we briefly review the advances of trait-based approaches in
162 community ecology and related fields to determine how such approaches can support the
163 evolution of ideas in fisheries science.

164 **1.1 Use of trait-based approaches across ecological fields**

165 Usage of trait-based approaches is increasing rapidly within ecology as a whole, but uptake of
166 these ideas is heterogeneous among subfields (Fig. 2). The modern origins of trait-based
167 approaches arose from plant community ecology (Lavorel & Garnier, 2002; McGill et al., 2006;
168 Westoby & Wright, 2006), and this remains the most active field using trait-based methods. At a
169 broader scale, trait-based approaches appear more commonly in terrestrial than aquatic literature.
170 In aquatic fields, plankton community ecology is an early-adopter of trait-based methods
171 (Litchman & Klausmeier, 2008; Litchman, Klausmeier, Schofield, & Falkowski, 2007; Litchman
172 et al., 2010). Trait-based approaches have seen little use in fisheries science aside from indirect
173 connections through basic fish ecology (Stuart-Smith et al., 2013), particularly in stream
174 (Frimpong & Angermeier, 2010) and coral reef systems (Mouillot et al., 2013), and analysis of
175 marine organismal size distributions (Andersen, Jacobsen, & Farnsworth, 2015; Kerr & Dickie,
176 2001; Kiørboe et al., 2018; Sheldon & Parsons, 1967; Sheldon, Prakash, & Sutcliffe Jr, 1972).

177 Community ecologists have rapidly popularized the idea of using trait-based approaches
178 to seek general answers to the fundamental ecological question of what drives patterns of
179 community structure in space and time (McGill et al., 2006). Such efforts aim to reconnect
180 intraspecific and interspecific trait variation to niche concepts (Hutchinson, 1957; MacArthur &
181 Wilson, 1967) and modern coexistence theory (Chesson, 2000), and seek to explain community
182 assembly (Ackerly & Cornwell, 2007; Violle et al., 2012) and response of ecosystem structure
183 and function to disturbance and environmental change in systems from forests to coral reefs
184 (Mouillot et al., 2013). With such efforts has come the realization that the magnitude of

185 intraspecific and interspecific variation are more comparable in plant communities than
186 previously thought (Kattge et al., 2011; Messier et al., 2010). Since individual variation can
187 change the expected outcome of ecological interactions (Bolnick et al., 2011), it is perhaps not
188 surprising that this renewed focus on individual variation has led to different insights than
189 provided by the more typical approach of comparing mean characteristics among species (Violle
190 et al., 2012). If this refreshed perspective on intra- and inter-specific variation is applied to fish
191 communities, there could be profound insights for basic fish ecology regarding the contributions
192 of biotic and abiotic interactions to aquatic food web structure and how energy fluxes vary in
193 space and time with environmental change (see sections 2.2-3.2).

194 Trait-based approaches are not only influencing the basic ecological sciences, but also
195 applications to restoration and management. Trait-based methods are facilitating the
196 understanding of how ecosystem function and services are related not only to species diversity,
197 but to the distribution of functional traits within communities (Enquist et al., 2015; Laughlin,
198 2014). For example, Laughlin (2014) proposed a framework of trait-based models to explore the
199 most efficient paths to achieving restoration targets described with functional traits by using
200 assemblage structures to define target and actionable benchmarks to improve ecosystem
201 function. Researchers are using a similar mapping of biodiversity, traits, and function to predict
202 change in ecosystem function under a variable environment (Enquist et al., 2015). Analogously,
203 fisheries managers could define aquatic community structures that maximize sustainable fishery
204 yield and use these as biological reference points to implement EBFM (see sections 2.3, 3.3).

205 Following on the trait-based revolution in plant community ecology, researchers in a
206 broad array of systems are calling for advancement in their field through incorporation of trait-
207 based approaches. Fungal ecologists have a vision that these approaches and development of
208 relevant databases will advance their ability to describe life-history variation, succession, and
209 spatial community structure (Aguilar-Trigueros et al., 2015; Chagnon, Bradley, Maherali, &
210 Klironomos, 2013). Similarly, microbial ecologists are promoting trait-based approaches to
211 explore life-history variation and estimate biodiversity-ecosystem-function relationships (Krause
212 et al., 2014). In wetland plant ecology, extensions of terrestrial plant trait-based approaches
213 could help identify traits that drive ecosystem service provisioning (Moor et al., 2017).
214 Applications such as these have use in the field of fisheries, enabling translation of life-history
215 variation directly and efficiently into effects on stock productivity and catch limits in space or

216 over time (see section 2.1). The above are just a few examples of how bringing trait-based
217 approaches to new fields can provide novel insight and perspective. The following sections
218 describe our vision for how an infusion of trait-based approaches in fisheries offers similar
219 benefits as those seen in other disparate fields.

220 **1.2 Current and past use of trait-based perspectives in fisheries**

221 Aquatic populations and the individuals that compose them present sampling challenges different
222 from many plant and terrestrial animals. In addition to the difficulty of direct visibility and three-
223 dimensional movement capacity, surveys of marine species often remove individuals from their
224 habitat (via capture) and require destructive sampling that eliminates the opportunity to
225 determine how traits vary over time within individuals (e., repeated measures).

226 Despite the limitations and challenges of sampling the aquatic system, individual traits
227 were recognized by early fisheries researchers as an important source of information to
228 determine the processes driving observations of large fluctuations in fisheries catches (Smith,
229 1994). Specifically, the size and maturation state of individuals provided insight into variation in
230 reproductive potential (Holt, 1891, 1895) and cohort strength and distribution (Hjort & Petersen,
231 1905). The hypotheses and theories that emerged became the foundation of the rapid
232 advancement of ecological and population modelling and parameter estimation that began in the
233 early-to-middle 20th century (culminating in Beverton & Holt, 1957; Kingsland, 1995; with
234 earlier work reviewed by Quinn, 2003).

235 Biomass dynamic models and size- or age-structured models (using population- level
236 parameters determined outside the model) were the most prevalent fisheries modelling
237 approaches for decades, though approaches such as catch curve and length frequency analysis
238 were explicitly trait-based (Gulland, 1983; Quinn & Deriso, 1999). Formal inclusion of traits in
239 fisheries models emerged with the development of size- and age-structured integrated population
240 models (Fournier & Archibald, 1982; Maunder & Punt, 2013). These models are fit to a variety
241 of data, including individual-level metrics like size at age and maturity, to estimate population
242 parameters and predict stock status (Dichmont et al., 2016; Methot & Wetzel, 2013). Trait
243 information is highly valued in these models, often improving estimation of dynamics (Wetzel &
244 Punt, 2015) and enabling the modelling of coarse intraspecific variation in growth over space or
245 time (Methot & Wetzel, 2013; Taylor & Methot, 2013).

246 As fisheries science focused mainly on population modelling, patterns and theory of life
247 histories started emerging (Beverton & Holt, 1959). Note that although life-history
248 characteristics were often referred to as traits, they do not meet our trait definition here.
249 Nonetheless, relationships between growth, longevity, mortality and reproduction were used to
250 produce predictive life-history patterns (Charnov, Gislason, & Pope, 2013; Then, Hoenig, Hall,
251 & Hewitt, 2015; Thorson, Munch, Cope, & Gao, 2017). These patterns were combined to form
252 life-history strategies (e.g., slow growing, long-lived, opportunistic strategists; Adams, 1980;
253 King & McFarlane, 2003; Winemiller & Rose, 1992), all dictated by population level
254 parameters, but implicitly driven by traits (Chapman & Robson, 1960; Roff, 2002; Stearns,
255 1992). Increasingly, researchers are recognizing the importance of incorporating individual
256 variation in estimation of growth, mortality (e.g., e.g., Jacobsen, Essington, & Thorson, 2018;
257 Laslett, Eveson, & Polacheck, 2004; Pilling, Kirkwood, & Walker, 2002; Sinclair, Swain, &
258 Hanson, 2002; Wang & Ellis, 2005) and reproduction (Rowe, Hutchings, Skjæraasen, &
259 Bezanson, 2008; Scott & Heikkinen, 2012). This is particularly true as it relates to the increasing
260 interest in the influence of environment, habitat (Hutchings et al., 2007; Morrongiello &
261 Thresher, 2015) and fishing (Lowerre-Barbieri, Ganas, Saborido-Rey, Murua, & Hunter, 2011;
262 Wang, Chen, Hsu, & Shen, 2017) on the relative success of alternative life-history strategies
263 among individuals within a population (Conover, Arnott, Walsh, & Munch, 2005).

264

265 **2. Potential applications for trait-based fisheries biology**

266 Given the demonstrated utility of trait-based methods in community ecology we highlight a few
267 potential applications of trait-based methods in fisheries biology. We emphasize how modeling,
268 monitoring, and managing based on traits such as individual size can facilitate better
269 management outcomes.

270 **2.1 “Parameters that aren’t” and time-varying processes**

271 For over six decades, fisheries scientists have relied on fitting models to data under the
272 assumption that many processes can be approximated using life-history parameters that are
273 constant over time; however, many processes (e.g., somatic growth and natural mortality) clearly
274 vary among years due to density dependence and environmental variation (Thorson, Monnahan,
275 & Cope, 2015). Therefore, population parameters are increasingly understood to actually be
276 variables, and ideally, they are predicted from dynamics operating at the level of individual

277 decision-making and fitness optimization. Hilborn and Walters (1992, pg. 347) called this
278 phenomenon “parameters that aren’t,” and it remains one of the largest issues in fisheries
279 population dynamics (e.g., Sampson & Scott, 2012). Certainly, stock assessment scientists often
280 update parameters as new information becomes available and sometimes use empirical estimates
281 to inform time-varying vital rates; yet this approach is constrained by access to data and
282 appropriate statistical techniques and is potentially confounded by simultaneous changes in
283 exogenous factors such as fishing mortality and selectivity. Recent advances in state-space
284 models are making it increasingly feasible to predict time-varying parameters (using temporal
285 covariates or residual-error terms), but simply estimating additional random-effects (i.e.,
286 allowing slopes to vary with time) does not resolve the larger question: Why do parameters
287 change, and how can we efficiently measure such changes from field observations?

288 We therefore predict great benefits from using functional traits (as measured from field
289 samples) to mechanistically inform time-varying parameters as specified in population models.
290 For example, researchers have found that they can better predict recruitment using realized
291 spawning output rather than spawning biomass estimated from fixed size-fecundity relationships
292 in population models (Morgan, Perez-Rodriguez, & Saborido-Rey, 2011). Therefore, annual
293 sampling for traits like ovary weight and development, adult lipid concentration, and
294 reproductive investment (e.g., spawning frequency) will often improve recruitment predictions
295 for fish populations. Similarly, changes in weight-at-length (a trait called “condition”) is likely to
296 indicate changes in resource availability or abundance of competitors. For example, recent large
297 increases in abundance of Baltic cod (*Gadus morhua*, Gadidae) were associated with decreasing
298 condition (Svedäng & Hornborg, 2014). In some cases, a large decrease in body condition could
299 indicate environmental conditions that are sufficiently poor to cause adult starvation and an
300 associated increase in natural mortality (e.g., for Gulf of Alaska Pacific cod (*Gadus*
301 *macrocephalus*, Gadidae) during the 2014-2016 marine heatwave, Barbeaux et al., 2017, see
302 Figs. 2.23-2.26). Furthermore, trends in natural mortality can be detected from survey data of
303 length or weight data alone when combined with basic catch information, leading to improved
304 estimates of population biomass and the drivers of biomass dynamics (Jacobsen et al., 2018). In
305 cases where a theoretical link exists between a trait and more than one biological process (e.g.,
306 body condition affecting both natural mortality and reproductive output), analysts could explore

307 models that include one or the other linkage and base resulting management advice upon an
308 ensemble of both models.

309 **2.2 Expanding the role of traits in fisheries management: towards trait-based harvest** 310 **control rules and ecosystem indicators**

311 Fisheries management scientists use trait-based methods intermittently, and greater recognition
312 of existing trait-based management could lead to improved coordination of research and
313 management changes among regions. For example, fisheries researchers and managers already
314 consider traits when discussing: (1) protection of forage fishes, (2) maintenance of size diversity
315 and ecological integrity more generally, and (3) consequences of global change.

316 An active debate is whether rates of fishing should be lower for “forage fishes” than that
317 recommended from single-species assessment models. Advising lower fishing rates for forage
318 fishes is often justified by claims that their abundance and nutritional density supports
319 productivity of many predators (Alder, Campbell, Karpouzi, Kaschner, & Pauly, 2008; Pikitch et
320 al., 2012; Pikitch et al., 2014; Trites & Donnelly, 2003). Forage fishes are often defined as
321 species having a low maximum age, small asymptotic size, and low trophic position within a
322 community (Rountos, 2016). Fisheries managers are therefore discussing whether management
323 actions should protect species with typical trait values (small body sizes) that correlate with
324 ecological function (high production per biomass; Engelhard et al., 2014). Fisheries managers
325 concerned with predator forage could instead modify management measures to achieve a target
326 biomass of small-bodied individuals, without explicit consideration of the species comprising
327 these individuals (i.e., including juveniles of species with larger asymptotic body sizes). Another
328 relevant trait distinction that managers might consider is separate measures for demersal and
329 pelagic forage fishes, or targeting management actions based on functional traits that define
330 positions of individuals in food webs (as opposed to the mean trophic level of a species).

331 Similarly, fisheries managers in Europe and elsewhere have increasingly discussed a
332 “stop-light” approach. This refers to management based on community-level control rules
333 derived from threshold responses in indicators of change in ecosystem structure (Jennings,
334 2005), which are often related to size structure (Greenstreet et al., 2011; Houle, Farnsworth,
335 Rossberg, & Reid, 2012), e.g., the Large Fish Indicator, slope of the size spectrum, or mean body
336 length. This community-level control rule can be interpreted as an effort to maintain diversity in
337 a functional trait (individual size), and we foresee future efforts to maintain functional diversity

338 or desired forms of trait distributions in a range of traits and life-histories (Pecuchet et al., 2017).
339 Likewise, fisheries management councils in the United States are increasingly interested in
340 results from integrated ecosystem assessments (Levin, Fogarty, Murawski, & Fluharty, 2009;
341 PFMC, 2013), and ecosystem assessments in the future may include trait-based management
342 indicators.

343 To implement trait-based ecology into management of marine resources, target reference
344 points for indicators need to be set for trait-distributions, on the level of stocks and ecosystems.
345 These targets need to be agreed upon with collaboration among stakeholders, managers, and
346 scientists. Involvement of managers and stakeholders is important for collaboration, data
347 collection, and development of robust trait-based indicators. Many trait-based targets are set by
348 reference to unfished states (e.g., size spectrum slope or age distribution within a stock), and
349 since these are rarely available from empirical data, efforts in modeling and theoretical ecology
350 are required to set baseline values. A major challenge for scientists is to communicate and
351 develop target values of trait indicators.

352 A practical application of trait-based management to fisheries would benefit
353 contemporary efforts to move towards ecosystem-based fisheries management (Skern-Mauritzen
354 et al., 2016). Trait-based applications can be used as specific tools to meet national and
355 international legislation and agreements. Potential candidate traits for ecosystems are size
356 distributions, trait diversity, or prevalence of specific desired traits. An example where direct
357 application of a trait-based framework is useful is the European Marine Strategy Framework
358 Directive, which requires the use of indicators to reach ‘good ecological status.’ By being readily
359 measurable and potentially comparable using available historical data, trait-based indicators have
360 the potential to be an invaluable supplement to current management practices in this framework.
361 Additionally, trait distributions could be a valuable tool for management in terms of observing
362 gradual ecosystem change due to a variety of anthropogenic impacts, including overfishing and
363 climate change.

364 Climate change presents a major challenge to fisheries management, where there is much
365 room for improvement in how climate information is used across the science-policy interface
366 (Karp et al., 2019). Climate influences fish at the individual level where, e.g., temperature
367 influences metabolism and growth according to a thermal tolerance function. As a result of this,
368 environmental trends can influence stock productivity and distribution along with the ability to

369 detect such changes via monitoring and population modeling. Recent recommendations for
370 incorporating climate in fisheries management include establishing mechanistic drivers of
371 biological change, accounting for intraspecific variation, and the expansion of monitoring efforts
372 for the rapid detection of responses to a changing environment (Karp et al., 2019), all of which
373 are strengths of the trait-based approach. Monitoring changes in traits across an ecosystem will
374 be important to measure complex system-level responses to global change (Kiørboe et al., 2018),
375 informing decisions such as the reduction of catch limits because of decreases in ecosystem
376 productivity. Specifically, changes in traits such as body condition or metabolic rates (as
377 measured by, e.g., RNA expression and hormone concentrations) may be useful indicators of
378 regional environmental changes that otherwise may be obscured when only inspecting species-
379 by-species responses. Trait monitoring programs would complement ongoing efforts to
380 categorize the intrinsic vulnerability of species to climate change (Hare et al., 2016) through
381 rapid detection of climate-driven changes in productivity and community structure.

382 **2.3 Trait-based models to inform ecosystem-based management**

383 Management of marine resources has improved drastically in recent years (Worm et al., 2009),
384 but this is mainly due to increased attention to rebuilding overfished stocks on a single species
385 level (Hilborn & Ovando, 2014; Wetzel & Punt, 2016). Even though ecosystem-based fisheries
386 management (EBFM) has been promoted for over a decade (Pikitch et al., 2004), it has still
387 struggled to make an impact on tactical management (Skern-Mauritzen et al., 2016).

388 Multispecies trait-based models can provide strategic guidance to inform future tactical
389 applications of EBFM by predicting the influence of fishing and climate change on ecosystem
390 structure and function.

391 A common problem in ecosystem modelling is the accelerating rate of increase in the
392 number of estimated parameters given an increase in the number of modeled species. For
393 example, an ecosystem model that estimates all pairwise species interactions will have N^2
394 interaction parameters for N species. This increase in model complexity ultimately causes large
395 structural uncertainty (Collie et al., 2014). A suite of models commonly referred to as ‘size
396 spectrum models’ remedy this by expressing the community state as a distribution of abundance
397 of traits rather than taxonomic units (Blanchard, Heneghan, Everett, Trebilco, & Richardson,
398 2017). Individual body size is often the trait used to describe community state (Andersen,
399 Jacobsen, et al., 2015) because this trait influences metabolic rates (West, Brown, & Enquist,

400 1997), prey size (Barnes, Maxwell, Reuman, & Jennings, 2010; Gilljam et al., 2011), swimming
401 performance (Ware, 1978) and the biomass distribution of individuals (Sheldon & Parsons, 1967;
402 Sheldon et al., 1972). The assumption that individual body size governs community processes
403 can result in a model with a fixed number of parameters regardless of the number of species. We
404 introduce size-spectrum models below as an example of trait-based ecosystem modelling, while
405 noting that some current applications of these models are not entirely trait-based (e.g., in cases
406 where asymptotic size is defined for each species).

407 Size spectrum models are structured physiologically, where encounter rates (leading to
408 feeding and subsequently growth), mortality, and reproduction are calculated on the level of the
409 individual (as a function of their size). These sub-models are often scaled up to the population
410 level using the McKendrick-Von Foerster equation

$$411 \quad \frac{\partial n(w)}{\partial t} + \frac{\partial g(w)n(w)}{\partial w} = -\mu(w)n(w)$$

412 where $n(w)$ is the number of individuals at weight w , a vector of which describes the size
413 spectrum, t is time, g is growth rate and μ is mortality. The equation is supplemented by a
414 boundary condition $g(w_0)n(w_0) = R$, where R is the number of recruits entering the population
415 per unit time. It is clear from the McKendrick-Von Foerster equation that the rate of change in
416 numbers in a weight class (the first term on the left-hand side) depends on two things: how many
417 die before they grow larger (the term on the right-hand side), and how many grow into the next
418 size class (the second term on the left-hand side). In the dynamic population model, researchers
419 can specify recruitment, growth or mortality to vary over time (depending on the number of
420 conspecific adults, predators and prey).

421 The simplest multispecies size-spectrum models assume that there is no difference
422 between species, and therefore individual size determines rates of growth, mortality, and
423 reproduction. This simple ecosystem model is termed ‘the community model’ by Andersen et al.
424 (2015). These models are most often used to test the sensitivity of size spectra to, e.g., fishing
425 (Rochet & Benoit, 2011), life history diversity (Zhang, Thygesen, Knudsen, & Andersen, 2013),
426 and the prevalence of different feeding pathways (e.g., benthic or pelagic; Blanchard et al.,
427 2009).

428 Size-spectrum models can also be defined to include differences in asymptotic size
429 among species, using this difference to drive differences in age-specific growth, mortality (due

430 to, e.g., predator gape limitation), and reproductive rates among species (Andersen & Beyer,
431 2006; Gislason, Daan, Rice, & Pope, 2010). The inclusion of asymptotic size allows the models
432 to distinguish species and specify recruitment as a function of the abundance of mature
433 individuals within asymptotic size groups. The models track biomass moving through size
434 classes by growth and predation, and are therefore suitable to predict, e.g., how community
435 structure and fishery yield is influenced by size-selective fishing (Andersen & Pedersen, 2010;
436 Houle et al., 2012; Jacobsen et al., 2014) different forms of density dependence (Maury &
437 Poggiale, 2013), or climate change (Blanchard et al., 2012). Furthermore, the models have been
438 applied to several large marine ecosystems to predict efficient ecosystem level fishing patterns.
439 These applications inform strategic EBFM by quantifying the trade-off between yield and
440 ecosystem state, through incorporating biotic interactions between different sized individuals and
441 how they are affected by fishing (Jacobsen et al., 2017).

442

443 **3. Framework for trait-based analysis in fish conservation and management**

444 Trait-based approaches could have an important role in the management of marine resources in
445 both data rich and data limited systems. Trait based methods would serve as a complementary
446 tool to traditional single-species management while contributing to the developing field of
447 ecosystem assessment. We envision three steps for developing a trait-based approach to fisheries
448 management: (1) identify candidate traits; (2) screen for useful traits; (3) identify management
449 actions and reference points (see Fig. 3). The major challenges to implementing this framework
450 would be the transitions between steps: establishing the relationship between candidate traits and
451 the process of interest (from step 1 to 2), and the sampling logistics of monitoring the selected
452 traits (from step 2 to 3). Only the former challenge is unique to the trait-based approach, while
453 the latter is common to all management approaches. In practice, we envision that these steps
454 would be conducted as part of a system of iterative learning, where steps 1-3 are revisited
455 periodically to reflect lessons learned during previous iterations (Williams, 2011).

456 **3.1 Step 1: Identify candidate traits**

457 To apply the trait-based approach to fish conservation and management, the first step is to
458 identify candidate traits to measure. Candidate traits should be functional, thus one could start
459 listing traits likely to influence species fitness based on direct evidence or general first principles.
460 In addition to body size, we recommend listing other traits that affect survival, growth, or

461 reproduction through mechanisms such as predator defense. For example, changes in survival
462 could be measured by extent of armoring (Fig. 4), chemical defense (e.g., toxin concentration),
463 or body morphology (e.g., crypsis or ability to flee). In addition, we recommend consideration of
464 traits that integrate over many biological and physical processes to provide a fitness indicator
465 (e.g., lipid concentration or body condition). It may be prudent to select traits that can affect key
466 ecosystem functions, such as gape size (indicating capacity for top-down control) or the
467 morphology of habitat-forming species (indicating sheltering capacity). It is also helpful to
468 identify traits that researchers can quickly and precisely measure in a cost-efficient way over
469 large spatial scales.

470 **3.2 Step 2: Screen traits**

471 After identifying potential traits and making preliminary measurements, the next step is to screen
472 for useful traits given research and management goals. We recommend retaining any trait with
473 sufficient variation that satisfies at least one of the following conditions:

- 474 1. *Traits are directly useful*: Some traits tie directly into a given research or management goal.
475 For example, freshwater fisheries management often seeks to optimize angler satisfaction,
476 and therefore a time-series of “trophy-sized” catches will be useful as a direct measure of
477 management success (Gwinn et al., 2015). Similarly, wetland restoration often seeks to
478 minimize chemical contaminants in fishes targeted for consumption, so measuring chemical
479 concentrations will be directly relevant to determining further restoration efforts.
- 480 2. *Traits are known proxies for biological processes*: Traits that are not directly linked to
481 management outcomes may still be appropriate if they are reliable proxies for unmeasured
482 biological rates or processes. For example, individual size is correlated with metabolic rates
483 (West et al., 1997) and therefore excretion rates (Peters, 1986; Schindler & Eby, 1997). Thus,
484 measurements of community size-spectra can indicate changes in respiration and nutrient
485 cycling, and represent a measurable link between human actions (e.g., fishing) and
486 environmental degradation (e.g., eutrophication, acidification).
- 487 3. *Hypothesized mechanisms linking traits and biological processes*: Finally, researchers could
488 use ecological theory to hypothesize associations between traits and important biological
489 processes. These hypotheses could motivate future data collection and analysis to screen
490 traits that might later serve as “known proxies”. For example, natural mortality rate is an
491 important demographic parameter for population models and likely varies over time. Theory

492 suggests that immune burden is associated with senescence, and that high parasite
493 concentrations could indicate immune stress (Wilson et al., 2001) or behavioral modification
494 that may increase mortality risk (Lafferty & Morris, 1996). Therefore, researchers could
495 sample parasite concentrations for fishes of management concern (e.g., steelhead trout
496 (*Onchorhynchus mykiss*, Salmonidae) in the North Pacific) and explore the correlation
497 between parasite concentrations and demographic rates (e.g., Krkošek et al., 2011; in this
498 case, smolt-to-adult survival and repeat spawning frequency, indicating key survival rates).
499 In addition, information about parasite load has been used to estimate spatial population
500 structure and connectivity (Bailey, Margolis, & Groot, 1988; de Moor, Butterworth, & van
501 der Lingen, 2017; MacKenzie & Abaunza, 2014), which could inform spatial stock
502 assessment if researchers were able to link parasite burden to demographic rates.

503 **3.3 Step 3: Develop a management system using trait-based reference points**

504 Fisheries management generally compares a measure of system status (e.g., abundance) with a
505 target or limit reference level (e.g., abundance at maximum sustainable yield). Managers use this
506 comparison to regulate human activities (e.g., fishing) that influence resource status (Gavaris,
507 2009). We envision an implementation of fisheries management using a measure of system status
508 that is a mix of population-level attributes (e.g., population biomass) and individual traits (e.g.,
509 the shape of the size distribution). For example, ecosystem indicators could be a combination of
510 trait-based and species-based measures, such as multispecies maximum sustainable yield (MSY;
511 species based) or the slope of the size spectrum (trait based). Using individual traits as a
512 management indicator requires consideration of several questions:

- 513 1. *What is the desired system state?* Using a trait distribution (or a summary thereof) in fisheries
514 management requires defining a target and limit for that element. For instance, research
515 indicates that size spectrum slopes become steeper when fishing commences (e.g., Daan,
516 Gislason, G. Pope, & C. Rice, 2005; Fig. 3c). Management bodies must decide *a priori* on
517 acceptable targets (e.g., the expected size spectrum slope at multispecies MSY) and limits for
518 the ecosystem state. Some researchers have suggested that fishing on the ecosystem scale
519 should be distributed among sizes and species to maintain the ‘unfished’ size structure
520 (Garcia et al., 2012), defined as the size structure of a system without fishing. Whether the
521 unfished size structure is the desired state is up to the management body to decide, as other
522 solutions might give better results in terms of yield or profit while still being sustainable

523 (Jacobsen et al., 2017). Managers should develop this target state based on socio-economic
524 and biological considerations. Previous research has suggested guidelines for the process
525 used to design management targets (Rindorf et al., 2017), and these could be used to develop
526 trait-based target states.

527 2. *How best to measure system state?* Fisheries management must also measure system states
528 regularly to compare with system target or limit levels. To continue our example, we could
529 calculate community size spectra from scientific surveys that measure individual lengths. We
530 could also quantify distributions of other traits such as armoring (spine number or length),
531 chemical contamination or RNA/DNA ratios, but doing so would require incorporation of
532 novel sampling protocols in existing scientific monitoring programs.

533 3. *What policy would regulate human activities most effectively?* Fisheries management seeks to
534 achieve a target system state by regulating human activities using a well-defined and
535 transparent policy. Most regulations will involve some trade-off between multiple human
536 values (e.g., between economic value and risks of overfishing). These trade-offs are often
537 difficult to identify *a priori*, so fisheries science increasingly uses closed-loop simulation
538 with numerical models (termed “management strategy evaluation”, MSE) to evaluate
539 expected performance using alternative management policies. We recommend additional
540 research using MSE to identify what management policy is optimal to achieve a given trait-
541 based target.

542 Stock assessments are the science used to inform fishery management, and generally take the
543 form of a population dynamic model using life-history parameters (see Fig. 3a for examples)
544 rather than individual traits. However, researchers sometimes incorporate traits (averaged across
545 individuals in a given time) via samples of size or age composition samples (Methot & Wetzel,
546 2013) or stomach contents (Moustahfid, Link, Overholtz, & Tyrrell, 2009). Researchers could
547 incorporate traits into assessments in two additional and more fundamental ways:

548 1. *Monitoring status using predicted traits:* researchers could use stock assessments to predict
549 trait distributions, and then use the distributions as an index of population status. This would
550 build on existing length-based assessment methods (e.g., Hordyk, Ono, Valencia, Loneragan,
551 & Prince, 2015; Rudd & Thorson, 2018). For example, predicted changes in population age-
552 structure may be more sensitive to short-term changes in fishing intensity than would
553 changes in spawning biomass. Specifically, a prediction of strong recruitment will often be a

554 leading indicator of future changes in population abundance. Such forward-looking metrics
555 could help limit unnecessary abrupt change in recommended catches, which can cause large
556 socioeconomic costs.

557 2. *Defining system status using measured traits*: researchers can calculate management targets
558 as a function of field samples of traits. For example, the Large Fish Indicator (LFI) is
559 calculated directly from field samples of fish size as the proportion of fish greater than a
560 specified length (Cury & Christensen, 2005; Greenstreet et al., 2011). The LFI is used to
561 measure ecosystem status as an Ecological Quality Objective in the North Sea. In this case,
562 regions adopting the LFI can define a target based on ecological models and theory, e.g., 0.4
563 in the Celtic Sea (Shephard, Reid, & Greenstreet, 2011), and compare the current LFI relative
564 to this target within an empirical harvest strategy to inform management. Other trait-based
565 indicators could be used within empirical harvest control rules. For example, the proportion
566 of spawning male salmon that are jacks (i.e., young males) vs. fully grown males has been
567 discussed as an indicator for changes in the evolutionary pressures facing salmon stocks
568 (Gross, 1991), and could be used within an empirical harvest strategy (as either target or
569 limit) for exploited salmon stocks.

570

571 **4. How to advance trait-based ecology in fisheries biology**

572 In this paper, we briefly introduced trait-based approaches in community ecology, gave examples
573 of how it could be most useful in fisheries science, and outlined how it can be adapted to new
574 purposes. We now describe our vision of what would be required to “scale up” this trait-based
575 approach within fisheries science, in addition to the needs we highlighted earlier (development
576 and extension of trait-based ecosystem models, broad monitoring of traits, and methods for
577 defining trait-based management objectives).

578 **4.1 Creating and growing open trait databases**

579 Most importantly, we encourage more centralized storage, distribution, and documentation of
580 existing trait databases. Existing fisheries databases often include field measurements of only
581 population parameters (e.g., FishBase; Froese, 1990) or are specific to small subsets of fishes
582 (e.g., North American freshwater species in FishTraits; Frimpong & Angermeier, 2009). By
583 contrast to these population-level databases, a database of fish traits must include measurements
584 of individuals (not populations or species) with data regarding the species, location, and timing

585 of each measurement. In many parts of the world regional science agencies, survey teams, or
586 management bodies are already maintaining such databases for their particular system. For
587 example, the Northwest Fisheries Science Center has a public database of length and weight
588 measurements for hundreds of species collected in marine waters off the US West Coast
589 (<https://www.nwfsc.noaa.gov/data/map>) and the International Council for the Exploration of the
590 Sea has a similar database for European surveys (DATRAS ICES: [http://www.ices.dk/marine-](http://www.ices.dk/marine-data/data-portals/Pages/DATRAS.aspx)
591 [data/data-portals/Pages/DATRAS.aspx](http://www.ices.dk/marine-data/data-portals/Pages/DATRAS.aspx)). Without any centralized database for meta-data,
592 however, researchers rarely use these regional databases for comparative analysis outside of
593 small, geographically isolated areas. The importance of centralized meta-data for regional
594 databases is well-recognized for other activities in fisheries science (e.g., for regional ecosystem
595 analyses; Cisneros-Montemayor et al., 2016) in addition to marine ecology (Kjørboe et al.,
596 2018), and we similarly recommend a centralized database to provide access to (or ideally serve
597 and harmonize) data from regional trait databases.

598 Fisheries scientists also have a long history of compiling individual measurements used
599 in morphological identification of stocks using the dimensions or counts of body parts (Cadrin,
600 2000), such as fin rays, spines, teeth, gill rakers, etc. (collectively called morphometrics and
601 meristics). For example, WH Lenarz and colleagues recorded nearly 50 such trait measures for
602 thousands of individual rockfish (*Sebastes* spp., Sebastidae) off the US West Coast (PB Adams,
603 unpublished data). These individual measurements could be ecologically meaningful in some
604 cases, e.g., if a cline in the number of gill rakers is correlated with differences in feeding
605 behaviors within a species' range. Reliance on meristics and morphometrics for identification of
606 stocks has become much less prevalent since the advent of inexpensive genetic techniques, so we
607 fear that these historical datasets may disappear when researchers retire. We therefore see
608 urgency in developing a database of meristic and morphometric trait measurements for fishes.

609 **4.2 Incorporating novel traits**

610 In addition to historical (meristics, morphometrics) and common (length, weight) traits in
611 existing trait databases in fisheries science, we recommend research to expand the set of traits
612 that are typically measured in fisheries sampling programs. This could be done by applying the
613 workflow explained in Section 3 above (e.g., identify → screen → apply → repeat), and the
614 results will obviously vary among research groups based on their study species and scientific

615 goals. However, we here note several traits that appear particularly worthwhile for expanded
616 field sampling:

- 617 1. Researchers have shown that defense traits such as body armoring can indicate rapid changes
618 in exposure to predation (Fig. 4; Kitano et al., 2008). Future research could link such
619 measurements to historical databases of other morphometrics and meristics that relate to
620 predator defense, in which case it could provide a long time-series for identifying changes in
621 predation intensity.
- 622 2. The cost of measuring steroid hormone concentrations or even genetic expression is rapidly
623 decreasing (e.g., du Dot et al., 2009); therefore, hormone and gene-expression levels could be
624 measured to directly indicate opportunities for growth and exposure to natural mortality.
- 625 3. Autonomous sampling and automated compilation of large datasets (e.g., continuous
626 telemetry data from acoustic receivers) is providing researchers with new measurements of
627 behavioral traits. For example, acoustic sampling near fishing aggregating devices can now
628 measure the distance of individual tunas from the water surface or floating structures
629 (Moreno et al., 2016). These behavioral traits may indicate population-level changes in
630 vertical habitat that also influences mortality due to the extent of exposure to fishing or
631 predators.

632 We provide this list of examples to spark interest, and imagine that individual research groups
633 will identify other useful opportunities.

634 **4.3 Using traits to inform data-poor assessments**

635 Lack of available data to perform formal stock assessment prevails in the world of fishery
636 management. Researchers have confronted this challenge with a variety of alternative methods
637 developed to adapt to any data that is available (Carruthers et al., 2014). Several methods use a
638 hybrid of population parameters and trait-based inputs. For example, some methods use
639 individual length (Hordyk et al., 2015; Rudd & Thorson, 2018) or age (Thorson & Cope, 2015)
640 measurements (traits) along with life-history parameters to determine stock status .

641 While the above approaches use a mix of traits and parameters (much like typical stock
642 assessments), the management procedure approach to fisheries management (Geromont &
643 Butterworth, 2015) can be used to develop pure trait-based applications. Management procedures
644 use changes in indicators (e.g., an abundance index) to define decision rules that determine
645 modifications in catch or effort (Jardim, Azevedo, & Brites, 2015). Researchers could derive

646 these indicators of stock status from traits (see Section 3.3). Then, researchers could summarize
647 such indicators at the species or community level (Fontana, Petchey, & Pomati, 2016). The
648 management-procedure approach avoids modeling population dynamics, and therefore bypasses
649 the need to estimate population parameters. It can also combine different trait indicators to
650 provide multiple lines of evidence to inform management decisions (Dowling et al., 2015). If the
651 traits are easy to measure and prove to be an informative indicator, this simple approach can be a
652 powerful method to monitor and manage species when traditional data sources and coverage are
653 not available.

654 **4.4 Formal assessment of the costs, benefits, and potential pitfalls of trait-based**
655 **management**

656 It is important to acknowledge that adopting trait-based methods may not provide effective and
657 efficient improvements to fishery management in all cases, thus more formal scoping is needed
658 to determine the scenarios under which the approach is prone to success or failure. In some
659 cases, there will be additional costs associated with sampling traits, as even in regions with
660 existing fishery-independent surveys more time may be required to sample novel traits or
661 perform more comprehensive sampling of traditional body size measurements. There are also
662 additional costs when integrating these new techniques into current management regimes,
663 associated with funding researchers to formulate and test trait-based models while reconciling
664 differences in inferences between these and traditional population models; however, this problem
665 is ubiquitous to any new approach to ecosystem-based fishery management. There are also risks
666 of failure related to the potential for expected trends and relationships to be absent or difficult to
667 attribute to clear drivers, as it can be challenging to establish mechanistic links between changes
668 in traits and the environment. Sometimes there is little change in traits even over long periods,
669 despite clear changes in habitat and species interactions (Geladi et al., 2019). Finally, it can be
670 challenging to establish whether traits are truly functional, yet there is a developing literature
671 identifying traits that are generally related to fitness among fishes. In summary, most of the
672 challenges listed above are not unique to trait-based approaches, yet we encourage more formal
673 comparisons of approaches to demonstrate which questions and objectives would be most likely
674 to benefit from implementation of trait-based methods. Before suggesting replacing or
675 supplementing a population-based method with an analogous trait-based method we recommend
676 conducting cost-benefit and sensitivity analyses.

677

678 **4. Conclusions**

679 We call for incorporating the concept of functional traits into methods in fisheries science so that
680 we can build on innovations in other fields. This will allow us to address common challenges,
681 such as predicting ecosystem responses to environmental change, which require consideration of
682 variation among and within species. Trait-based approaches will help solve the issue of
683 increasing model complexity and associated uncertainty that has arisen as we develop the
684 scientific basis for EBFM, providing novel methods for assessing ecosystem status and
685 determining how ecosystem dynamics affect—and are affected by—fisheries. Trait-based
686 methods would complement traditional population methods to make management more agile,

687 able to quickly detect changes in underlying conditions that influence productivity, distribution,
688 and interactions. We present a framework for managing based on traits to demonstrate that such
689 advances are practical, feasible, and do not necessarily require radical shifts in philosophy or
690 decision-making structure. The evolution of trait-based methods can facilitate rapid advances in
691 fisheries, but this will require supporting new efforts, including: a commitment to systematic
692 measurement and screening of novel and familiar traits, in addition to development of open trait
693 databases, trait-based ecosystem models, and methods for integrating traits into descriptions of
694 resource status and reference points.

695

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1122

1123 **Table 1.** List of biological processes commonly used to predict fish population dynamics, with
 1124 examples of either (1) how that process could be measured as a trait at an individual level, or (2)
 1125 how that process can be estimated using a model that approximates a biological process when
 1126 averaging across multiple individuals with available data.

Biological process	Direct measurement (or a related proxy) of biological process for each individual	Model for process when averaging across individuals (with interpretable parameters for that model in parentheses)
Allocating energy towards reproductive output	Does an ovary contain mature oocytes?	Maturation ogive (represented by age/size at 50% maturity)
Accumulation of energetic reserves	Le Cren's (1951) condition factor	Ratio of asymptotic weight and asymptotic length
Individual somatic growth rates	Expression of growth hormones	von Bertalanffy growth curve (represented by the Brody growth coefficient)
Exposure to sources of non-anthropogenic mortality	Armor, body shape, change in age/size distribution	Survival function (represented by the natural mortality rate)
Opportunity to feed	Stomach fullness and	Predator-prey preference function

upon available prey resources	content, gape size, teeth or gill raker number or shape	(represented by relative attack rates); diet matrix for a population (represented by prey selection ratios)
Individual adaptations and behaviors to attain suitable habitat	Coloration, body shape, eye size	Habitat suitability model (representing relative preference for one or more environmental variable)

1127

1128

1129 **Figure Legends**

1130 **Figure 1.** Visualization of trait-based patterns across taxonomic scales and environmental
 1131 gradients, for three hypothetical species. The population approach often provides only a point
 1132 estimate for each species or population (A), which can obscure more nuanced patterns apparent
 1133 in intraspecific variation and scale of variation from among-individual to within-community (B).
 1134 Traits may vary with the environment (C), which can cause erroneous characterization of
 1135 differences in traits among groups, depending on what environment they are sampled in and how
 1136 many traits are being compared. For example, in panel B, it appears that the species represented
 1137 by black symbols (open and closed circles) are completely distinguishable based on two traits,
 1138 while the species represented by open circles and blue circles are moderately distinct, with some
 1139 overlap. This perspective obscures some information explained by the environmental gradient
 1140 (C), showing that both sets of species are have similar traits in some environments and differ in
 1141 others. As a result, if a study samples individuals only from a narrow subset of environmental
 1142 conditions (shaded region), then misleading generalities can arise (e.g., species represented by
 1143 black circles are completely similar and both are entirely distinct from the blue species). Fish
 1144 silhouettes are from <http://phylopic.org>. (Figure appears in colour in the online version only.)

1145

1146 **Figure 2.** Number of publications over time (A) with a topic (title, abstract or key words)
 1147 including the phrase “functional trait*” and a specific taxonomic group indicated in the legend,
 1148 and the general phrase “aquatic ecology” alone as a reference for the baseline growth rate of the

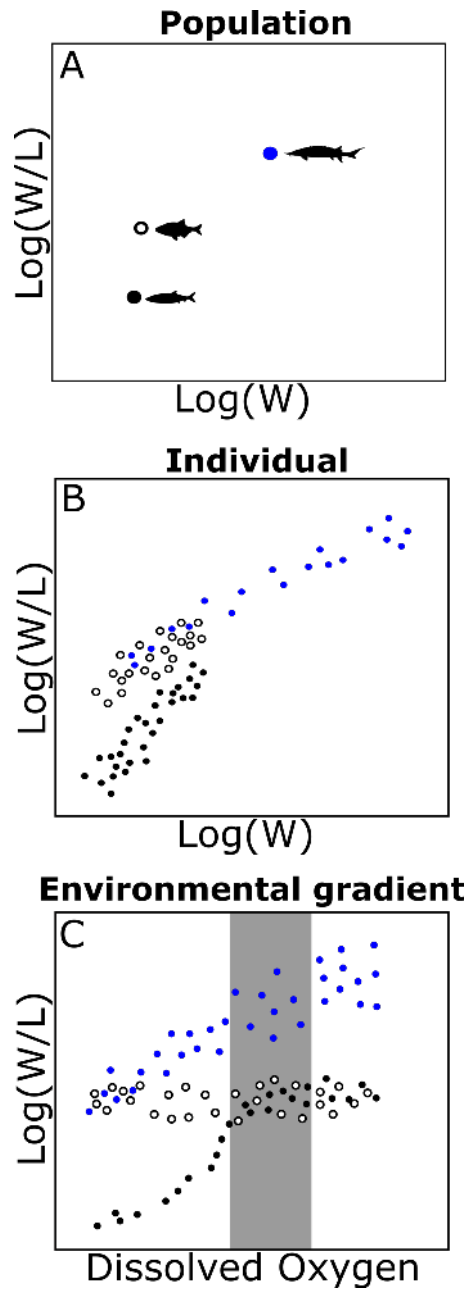
1149 literature. The number of citations of these papers over time (B). Results are from a search of the
1150 ISI Web of Science database for the years 2000-2016, conducted on 11/30/2017.

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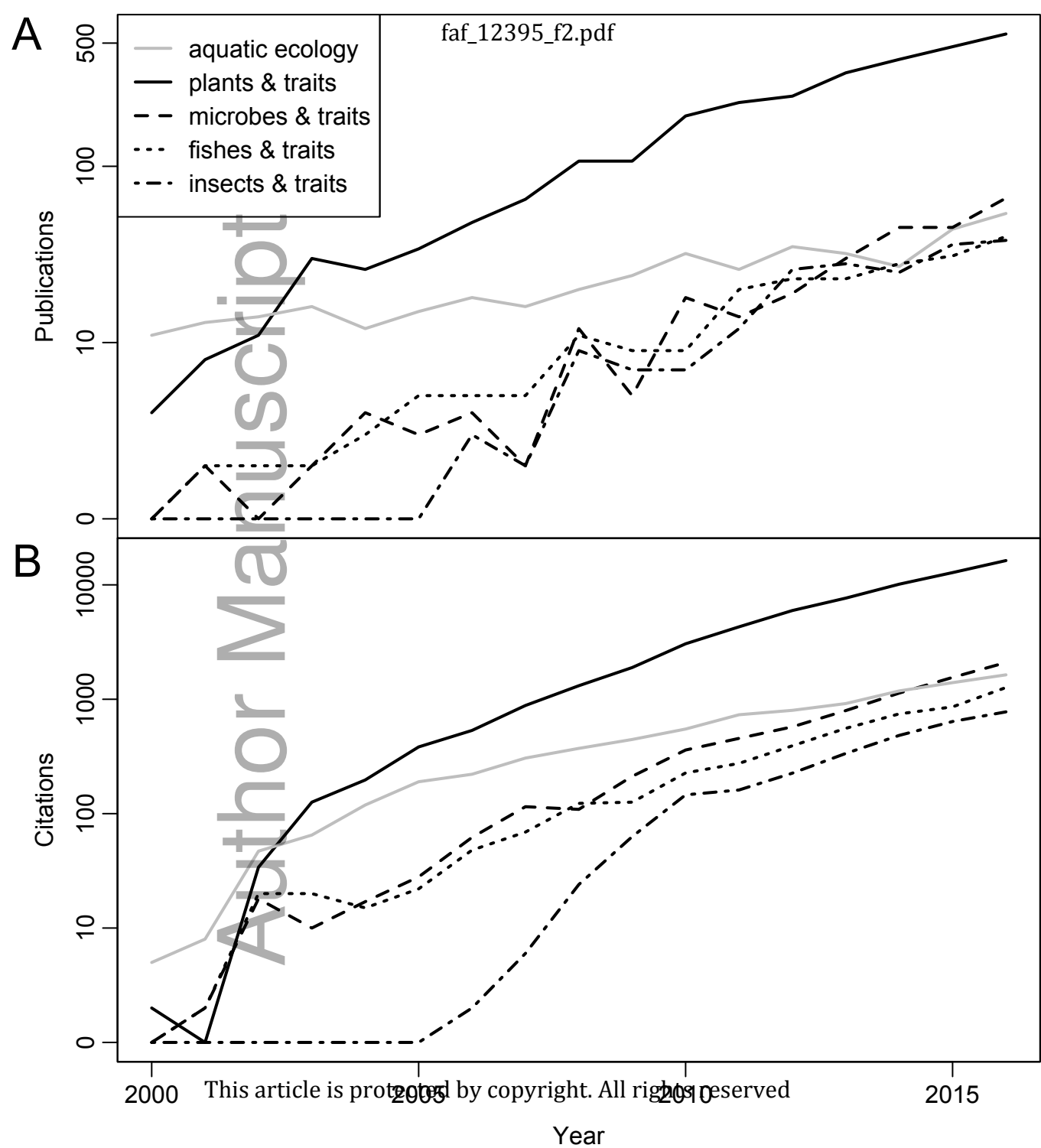
1152 **Figure 3.** Proposed framework for incorporating trait-based analyses in fish conservation and
1153 management. (A) Examples of how population parameters (blue text) are related to candidate
1154 traits (black text), which might be identified as part of the research component of a decision
1155 process for trait-based management (B). Once appropriate traits are identified, sampled, and
1156 screened, the management component of the framework will define the target and present status
1157 of the resource using a trait-based status designation. For example, (C) the size spectrum slope,
1158 serving as a trait-based ecosystem status indicator (solid line and points, with estimated trend and
1159 uncertainty) and a target reference point for a lightly exploited ecosystem (dashed horizontal
1160 line) – see the supplementary information for descriptions of the data and calculations. (Figure
1161 appears in colour in the online version only.)

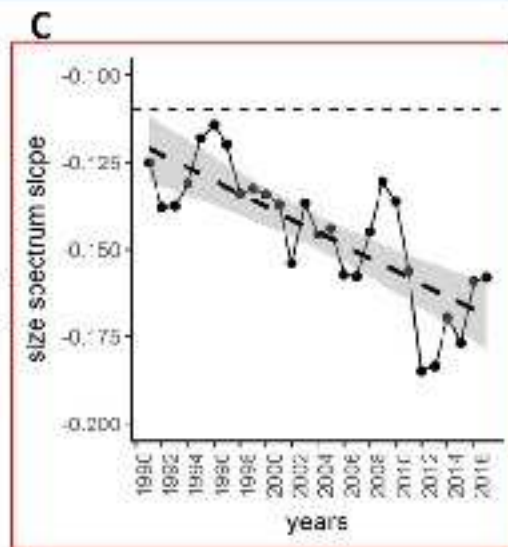
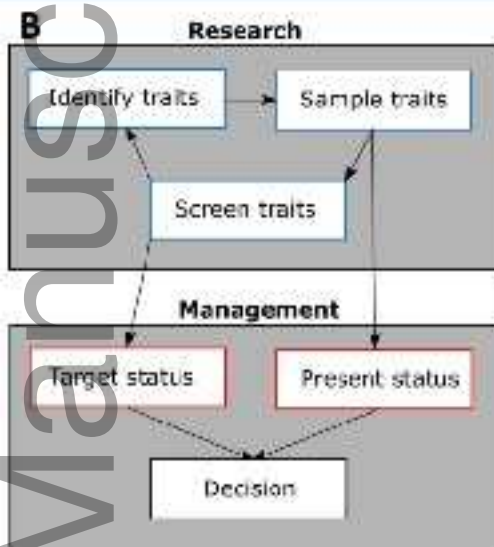
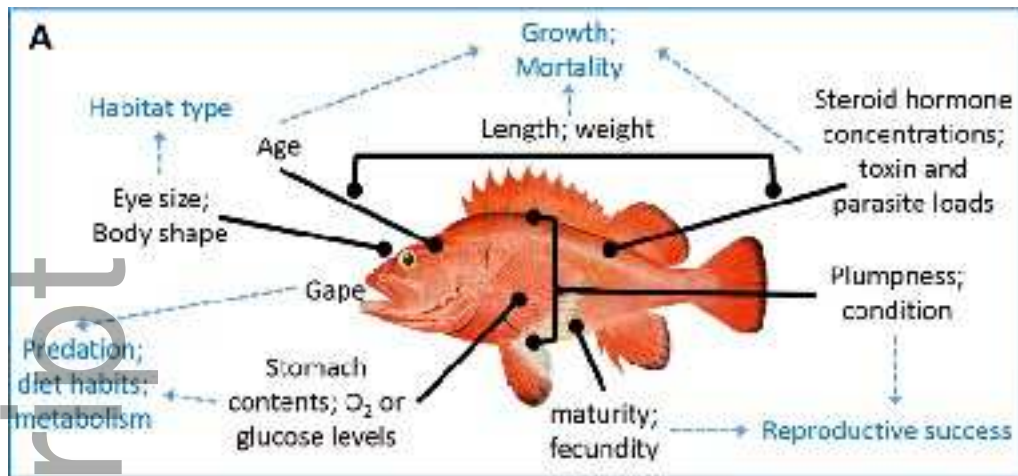
1162

1163 **Figure 4.** Changes over time in a predator defense trait demonstrate the utility of incorporating
1164 measures of a wide range of traits into monitoring programs. Threespine stickleback
1165 (*Gasterosteus aculeatus*, *Gasterosteidae*) in Lake Washington, Seattle, Washington dramatically
1166 increased their number of armor plates over several decades, possibly as a result of selection due
1167 to increased predation risk triggered by increases in water clarity. The figure is modified from
1168 Kitano et al. (2008) and reprinted here with permission. (Figure appears in colour in the online
1169 version only.)

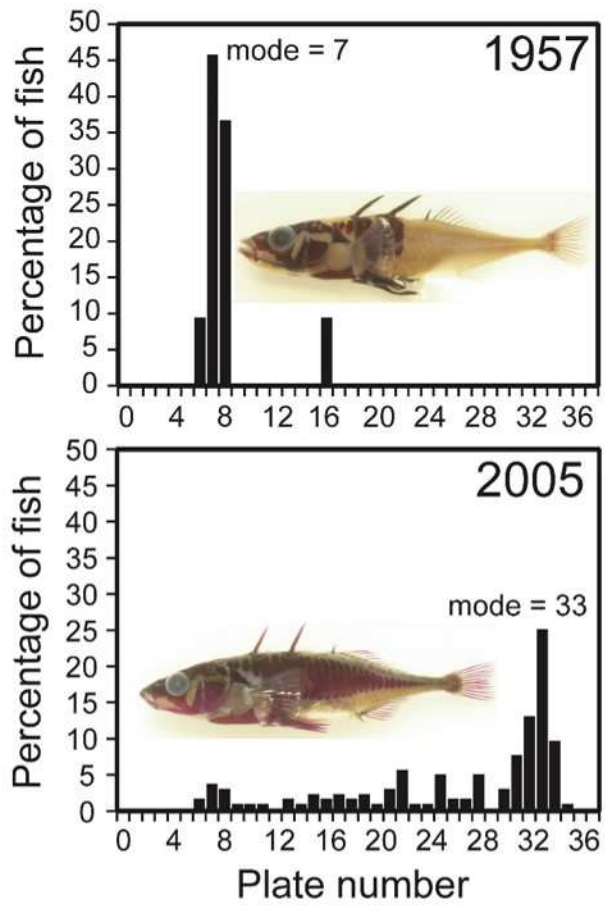


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